

XVII. *The structure and life history of Psychoda ser-punctata*, Curtis. By JOHN ALEXANDER DELL, B.Sc. Communicated by Prof. L. C. MIALL, F.R.S., F.E.S.

[Read May 3rd, 1905.]

*Habitat and Mode of Life.*

*Psychoda* in all stages of growth abounds throughout the year at the Leeds Sewage Works, and advantage has been taken of this circumstance to investigate more fully the life history of the insect. It obtains its food from heaps of coke, over which crude sewage is sprayed during the purifying process. The life which flourishes on the coke-heaps, and especially the bacterial life, effects the reduction of the sewage to a harmless liquid. Algæ, among which *Stigeoclonium tenue* is conspicuous, find here congenial conditions, and supply nutriment to insects of more than one kind. Besides *Psychoda*, a *Chironomus* and a beetle (*Platystethus*) occur. A *Scolopendra*, Mites, and *Nais* have also been observed on the coke-heaps.

The *Psychoda*-larva is minute, cylindrical, tapering toward the hinder end, and bluntly rounded in front. It may attain a length of 7.5 mm. The larva bears no locomotor appendages, but moves in a vermiform manner. On the fore part of the head are a pair of jaws, probably mandibles, which can be extended forwards, or folded backwards. By means of these and the recurved labrum food is crammed into the mouth. The last segment is usually bent upwards so as to keep its tip, which bears the only functional spiracles, clear of the semi-liquid filth in which the rest of the body is usually immersed. The pupæ are found together with the larvæ in the sewage.

The fly is small and of grey colour. The female is 4 to 4.5 mm. long, the male only 2.5 to 3 mm., including the wings. The male is further distinguished by the large genital appendages, which project from the extremity of the abdomen. The wings are longer than the body, which they completely cover, and slope when at rest. Both

body and wings are abundantly covered with grey hairs, which give the fly at first sight the appearance of a small moth, hence the name *Psychoda*. Round the edges of the wings are a few black tufts, and the veins are thickly covered with hairs. The hairy surface protects the body from accidental wetting. A fresh-killed fly, when pressed below the surface of the water, carries down with it so large a quantity of air, that on being released, it shoots at once to the top and remains floating. The flies may often be observed resting on the windows of empty houses, and are also abundant in privies, urinals, etc. At the Leeds Sewage Works they cluster on the under-side of the pieces of coke upon which the sewage is sprayed. They are sluggish, and do not readily take to flight. In returning from the sewage works to the University I have often found that the walk of three or four miles was insufficient to dislodge *Psychoda* flies which had clung to my dress. They can, however, run fast, and they are sometimes carried far by wind. The fly does not, so far as is known, feed at all.

In copulation the male runs alongside the female, stroking her with his antennæ, while the wings, antennæ and halteres are thrown into spasmodic vibration. The large forceps is then extended directly backwards, and the abdomen of the male bent round so that the hinder ends of the two bodies are brought into apposition. The forceps then close upon the body of the female, unless they miss, which not infrequently happens, as the male fly is unable to see what he is doing. In such a case the whole manœuvre is repeated. The males are apparently unable to distinguish which of their companions are females, as they very frequently attempt to copulate with one another. They have often been seen to die while still attached to the female.

As usual in *Nemocera* the eggs are deposited in an elastic, jelly-like mass. They are irregularly arranged in it, and unconnected with one another. The egg-mass thus formed is indefinite in shape, and may be fixed to a stone or other solid object. The total length of an egg-mass may be 1–2 mm., and such an egg-mass commonly contains 35–40 eggs. The eggs are small (·2 mm. to ·3 mm. in length) and sausage-shaped; they are opaque, and loaded with yolk-granules. Hatching takes place 10–14 days after laying, but may possibly be more rapid in a

warmer season than that in which my observations were made.

*Systematic position of Psychoda scarpunctata.*

The long antennæ of many similar joints, and the slender flexible maxillary palps, at once place *Psychoda* among the *Nemocera*. The absence of ocelli, the short and fleshy mouth-parts, the bead-like joints of the antennæ, the prominent genital forceps, and the structure of the wings characterize the *Psychodidæ*. The pattern of the wing-veins sufficiently indicates the genus *Psychoda*, while the black tufts on the margin of the wing distinguish the species *scarpunctata*.

*External features of the Larva*  
(Fig. 1).

The body consists of a head and eleven segments. Each of the first three segments is imperfectly divided into two annuli, and each of the remaining ones into three. The last segment is the only one which is extensively modified. The integument is covered with a thick layer of chitin, which is in places thickened into special protective plates. In general there is a thin membrane between the adjacent segments, and a longitudinal thin strip separating the dorsal from the ventral armour. The cuticle of a larva which has recently shed its skin is white and transparent, and such larvæ can be easily studied alive as transparent objects. As time goes on, however, the cuticle thickens, and a larva which has a moult in prospect becomes com-

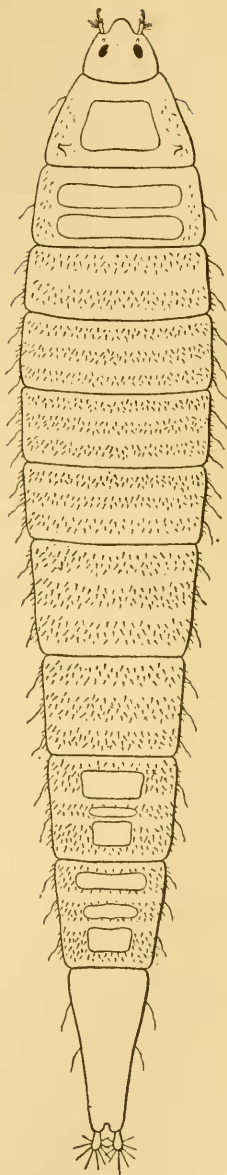


FIG. 1 (  $\times 20$  ).  
Dorsal view of larva.

pletely brown and opaque. From the middle of each segment a pair of lateral setæ project, which are more or less curved. There are also on all the segments except the first and second numerous short, rather blunt setæ, arranged in transverse bands; there are two of these bands on the third segment, and three on each of the others. In the mid-dorsal line of the ninth and tenth segments occur a series of black, oval, shining plates, transversely elongated, but not reaching the sides of the body. There are usually three on each segment, but they are irregular in form and size, and occasionally one is found on the eighth segment. The last or eleventh segment is smooth and hard, and tapers backwards, though

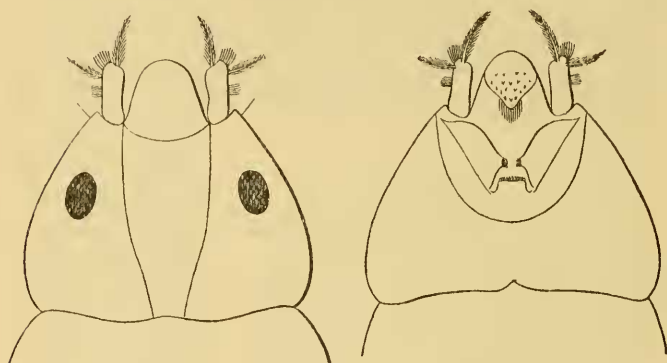


FIG. 2 (  $\times 80$  ).

Dorsal view of head of larva (to left); ventral view (to right).

the extreme tip is truncated. The anus opens on its under-side, in a recess at the attached end of the segment. There are two small appendages arising from the truncated terminal surface of this segment. They are short, fringed with setæ, and somewhat like the corresponding structures in the *Pericoma* larva, but not so much developed. As in *Pericoma*, the larvæ can hang from the surface-film by means of the anal appendages. If depressed beneath the surface, the anal appendages do not carry down a bubble of air, with which the spiracles communicate, as in the *Pericoma* larva, though small air bubbles often adhere to the setæ. When floating at the surface, the larva, if it is able to reach the bottom, can drag itself along by means

of the mouth-appendages, which are rapidly extended and closed, so as to scrape the bottom.

The head (Fig. 2) is subconical, much reduced, and partly retractile. It can be withdrawn into the prothorax, so that the head is concealed as far forward as the eyes. This position is temporarily assumed during crawling, and is normal in larvæ about to pupate. The head nearly resembles that of *Pericoma*\* and *Murina*.† In each case the mid-dorsal surface is occupied by the roughly triangular clypeus, flanked on either side by the large epicranial plates, which bear the black, shining, simple eyes, and the antennæ. The antennæ are even more reduced than in *Pericoma*, and are little more than knobs. The forward prolongation of the clypeus is the labrum. This is an elongated triangular organ; its apex is turned underneath in such a way that the tip lies almost directly beneath its junction with the clypeus. A few hairs arise from its anterior edges, and on the surface of the apical part, which is morphologically dorsal, but actually ventral, there occur a large number of backward-directed spines. On each side of, and immediately behind the labrum is an appendage, probably the mandible, which is short, and ends bluntly. From each appendage arise two large plumose setæ, one running forward, the other outward. There are also two bunches of shorter setæ. Immediately behind the supposed mandibles is a pair of semi-circular, plate-like appendages, which probably represent the maxillæ. Between them and in the median line is a comb-like organ with its teeth projecting forwards. A similar plate is common in *Nemoceran* larvæ, and has been identified with the submentum.‡

#### *Nervous System of the Larva.*

The nervous system (Fig. 3) consists of the usual cerebral ganglia and the ventral chain. The cerebral ganglia are pear-shaped, and from their pointed ends arise a pair of nerves, which run forwards into the head. The sub-œsophageal ganglia are, as usual, connected with the cerebral so as to form a ring round the œsophagus, through which runs the dorsal vessel. Behind these is a series of

\* Miall and Walker (1895).

† Müller (1895).

‡ Miall and Hammond (1892 and 1900).

eleven ganglia, not segmentally arranged. The hindmost of the chain is small, and close to the one immediately in front of it. The first body-segment contains, in addition to the first ganglion of the ventral chain, the cerebral and sub-oesophageal ganglia, which in most insects lie in the head. The shifting of these ganglia into the thorax is no doubt explained, as in the case of *Chironomus*, by the reduction of the larval head. The large and complex head of the fly cannot be developed within the small larval head, and its rudiments, besides the brain, which it will ultimately enclose, are transferred to the much more spacious prothorax.\*



FIG. 3.

Nerve-cord  
of larva.

#### *Alimentary Canal of the Larva.*

The alimentary canal resembles that of *Chironomus*† so closely that I shall merely describe the points of difference between the two. The fore-part of the stomach is separated as a cardia, but has no cæca. Between its wall and the reflected wall of the oesophagus arises a thin chitinous membrane, the "peritrophic membrane" of Balbiani.‡

The function of the peritrophic membrane is to protect the mesenteric epithelium from abrasion by inorganic particles, which the larva swallows along with its food. It is apparently cast periodically. In a living *Psychoda* larva reversed peristaltic contractions have been observed. The digested food has been seen to be carried up into the space between the peritrophic membrane and the mesenteric epithelium by these peristaltic contractions. At the hinder end of the mesenteron is a slight dilatation, into which open the five Malpighian tubules. Five is an unusual number of tubules among insects, but it is found in *Blepharoceridæ*, *Culex*, and *Ptychoptera*.§

There is a pair of salivary glands situated in the fore-part of the thorax. They are roughly bean-shaped, and the duct arises from the part corresponding to the hilum

\* Miall and Hammond (1892, 1900).

† Miall and Hammond (1900).

‡ Balbiani (1890).

§ Müller (1895).

of the bean. They are placed one on each side of the alimentary canal, which they partly encircle. The two ducts run forward beneath the alimentary canal, and unite in the posterior region of the head. The structure of the glands is very simple. They are hollow, the wall being only one layer of cells thick. The cells are very large, and possess very large nuclei, in which by suitable methods a distinct chromatic filament and nucleus can be made out. I have not been able to detect the elaborate nuclear structure of the salivary cells of the *Chironomus* larva.\* Outside the cells there is a thin basement-membrane.

### *Respiratory System of the Larva (Figs. 4-6).*

The respiratory system of the larva is well developed. The air is renewed mainly, if not altogether, by means of the large posterior spiracles (Fig. 6). These are situated at the apex of the last segment, close to the bases of the minute anal appendages. Each spiracle communicates with a large longitudinal trachea. Immediately within the spiracle the trachea is slightly dilated into an oval chamber, and the centre of this is occupied by an ovoid mass of chitin, attached to the walls of the chamber by chitinous threads. The whole arrangement forms a kind of loose spongy plug. In addition to this pair of large posterior spiracles, there are an anterior pair borne by two short processes on the sides of the prothorax (Fig. 4). They are not open, and probably not functional, since they are always immersed in water or mud. Leading into each spiracle is a trachea, which, as it passes into the process on which the spiracle is borne, gradually becomes spongy and takes on a black appearance as seen by the microscope, probably due to contained air.

There are two very large tracheæ (Fig. 4), each arising from one of the posterior spiracles, and running forward along the back. They are connected by a series of commissures, one of which occurs at the hinder end of every segment, except the last. In many cases small, forward-directed branches arise from the commissures. Some of these are connected with the alimentary canal, and on this account the commissures are very slack, especially those near the middle of the body. During the

\* Balbiani (1881).

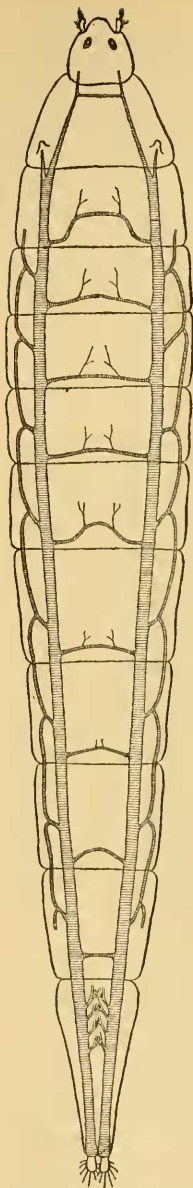


FIG. 4 ( $\times 20$ ).  
Tracheal system of larva.

vermiform movements of the animal there is a considerable amount of sliding of the alimentary canal and body-wall on one another, and a tight commissure would be liable to be snapped, or to tear the tissues. In each segment, besides the commissures, there is found a lateral branch running downward and forward, and soon splitting into three. Of these three each posterior branch unites with the

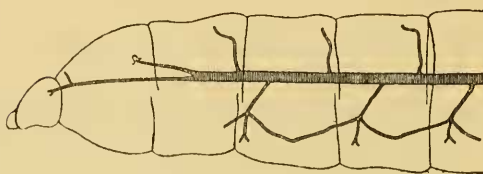


FIG. 5 ( $\times 20$ ).

Anterior part of tracheal system of larva,  
in side view.

anterior branch of the segment behind, thus forming a loop, while the middle branch breaks up into branches of distribution. In the last segment, immediately dorsal to the hinder part of the heart, there arise from each

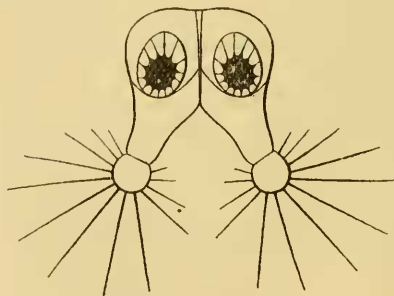


FIG. 6 ( $\times 100$ ).  
Posterior spiracles of larva.

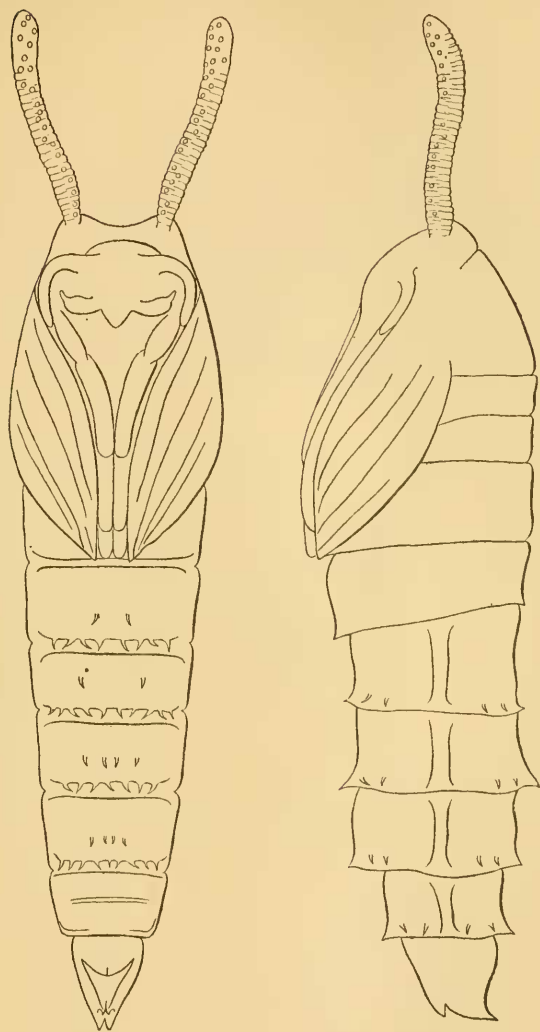


FIG. 7 (  $\times 20$  ).

Ventral view of pupa (to left) ; side view (to right).

longitudinal trachea a number of small branches, which break up into branches of distribution in the neighbourhood of the pericardium.

*Pupation: External Features of the Pupa.*

After reaching its full size, the larva becomes sluggish and ceases to feed; the head becomes retracted, so that the part behind the eyes is concealed by the first body-segment; the last larval skin is then shed, and the pupa emerges. This takes place while the animal is still buried in slime. In a short time the pupa makes its way to the surface, where it lies with the respiratory appendages exposed. This facilitates respiration, and the escape of the fly.

The pupa (Fig. 7) is, as usual, shorter and thicker than the larva. When it first appears it is white, but the cuticle soon thickens and turns brown. The head is not externally marked off from the rest of the body, but the compound eyes of the fly can be seen through the pupal skin. From the front of the prothorax arise the two respiratory appendages (Prothorakalhorn of De Meijere\*). They are rather less than one-third of the length of the body, and transversely wrinkled. Scattered over their surfaces, especially towards the distal end, occur numerous transparent circles, which appear to be holes, but are really thin spots in the cuticle. A shallow transverse furrow separates the prothorax from the mesothorax. The three pairs of leg-sheaths are straight, and reach the beginning of the third abdominal segment, where the tips of the wing-sheaths are also situated. All the exposed abdominal segments, except the eighth or last, are protected by dorsal and ventral plates, whose hinder margins end in rows of backwardly-directed spines. There are also a few scattered spines on both dorsal and ventral surfaces. Each spine is a pointed process of the body-wall. Its apex bears a spike set in a socket. The last segment bears four large spines, two terminal and two subterminal. The spines assist the pupa to move about in the filth in which it is buried, and so keep the respiratory appendages exposed to the air.

\* De Meijere (1902).

*Tracheal System of the Pupa* (Fig. 8).

The tracheal system of the pupa is closed, the contained air being renewed by means of the prothoracic respiratory appendages, a pair of hollow finger-shaped processes, which project forward from the prothorax. A tracheal extension (Fig. 9)—Hornfilzkammer of De Meijere—lies within the respiratory appendage. The structure of the wall of the pupal respiratory appendage is not unlike that of *Ptychoptera*. In places the tracheal extension bulges through the wall of the respiratory appendage, giving

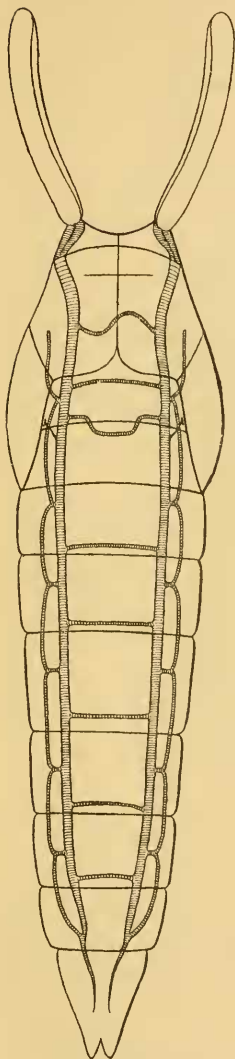


FIG. 8 ( $\times 20$ ).  
Tracheal system of pupa.

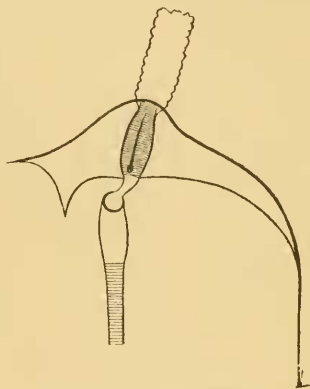


FIG. 9 ( $\times 40$ ).  
Tracheal extension of pupa.

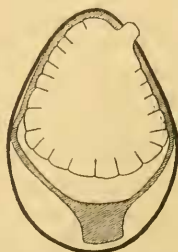


FIG. 10 ( $\times 100$ ).  
Transverse section of tracheal extension of pupa.

rise to the clear circular spots previously mentioned. Except at these places the tracheal extension is separated from the wall of the respiratory appendage by a space, in which sections show the presence of a tissue, affected by ordinary staining re-agents (probably the epithelium which secreted the tracheal extension). A transverse section shows scattered setæ projecting inwards from the wall of the tracheal extension (Fig. 10). Traced backwards, the tracheal extension passes through the space between the body of the fly and the pupal skin, and finally enters the body in the fore part of the mesothorax. There are two large, longitudinal tracheæ (Fig. 8) communicating directly with the tracheal extensions just described. They are connected by a series of nine commissures, one in the mesothorax, two in the metathorax, and one in each abdominal segment, except the seventh and eighth. There is also a series of lateral loops exactly like those of the larva. The first, however, which arises in the metathorax, runs through two segments; all the others run from one segment to the next. The longitudinal tracheæ end in tapering extremities in the last segment.

The tracheal system of the pupa is formed around that of the larva, and consequently in a larva about to pupate the walls of the tracheæ appear double. The longitudinal tracheæ of a late larva communicate with the pupal respiratory appendages, which are formed during this stage. The respiratory appendages are not modelled on any pre-existing larval organ, hence it is not surprising to find that the larval trachea, just behind the respiratory appendage, comes out through the wall of the pupal tracheæ, and makes its way to the prothoracic spiracle of the larva. It is also continuous with the base of the respiratory appendage. This makes a sharp angle with the larval trachea, and can be seen through the larval cuticle just in front of the larval prothoracic spiracle. Its distal end turns downwards, and almost touches its fellow of the opposite side in the mid-ventral line. In the pupa which has just shed the larval skin, the respiratory appendages lie close to the body, much as they do in the larva; but when the pupa makes its way to the surface of the mud, the respiratory appendages stiffen, and stand out clear of the surface. Pupæ can be easily detected in a sample of sewage, by their projecting respiratory appendages. A pupa, when kept in a bottle of water, is unable to rise to the surface,

or to breathe the air dissolved in the water, and dies in a few days.

*The Head and its Appendages in the Fly.*

The head is almost vertical. (Figs. 11 and 12.) Seen from above it is transversely oval; the front surface is pear-shaped, narrowing downwards to the labrum. The com-

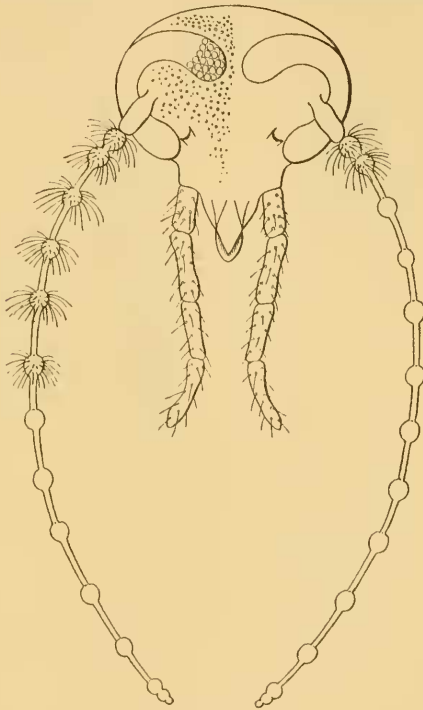


FIG. 11 (  $\times 80$  ).

Head of fly.

pound eyes are horse-shoe shaped, and nearly meet above. They contain comparatively few ommatidia, not more than five or six rows in the widest part, and possibly about eighty in all.

Immediately within the lower ends of the horse-shoe-shaped compound eyes can be seen in the openings of a pair of chitinous tunnels which perforate the head. They run through it obliquely, and their openings on the back of

the head are nearer to one another than the openings on the face. The tunnels are not of absolutely uniform diameter, though their variations are nowhere very great.

The antennary muscles, which are the only important muscles in the head, are attached close to the hinder openings of the chitinous tunnels, which seem to act as struts, and prevent the head from yielding when a strain

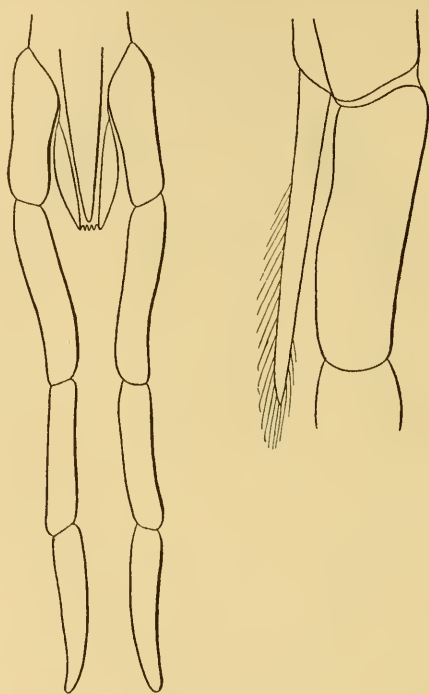


FIG. 12.

Ventral view of mouth-parts of fly (to left); maxilla in side view (to right).

is put upon it by the contraction of the antennary muscles.

Similar structures have been described in *Anopheles*, where a pair of straight chitinous tunnels perforate the head, and in *Chironomus*, where a pair of small openings on the face open into a pair of somewhat irregular chambers, which in turn open to the exterior by a pair of slit-like apertures on the back of the head.\*

\* Miall and Hammond (1900).

In the *Chironomus* fly the antennary muscles are attached to the walls of the chitinous invaginations themselves, an interesting point of difference from *Psychoda*. A somewhat similar pair of structures has been described in some other insects, notably in *Corydalis*.\*

Each antenna consists of fifteen joints; of these the first is cylindrical, the second globular, and the others flask-shaped, with the exception of the last three, which are globular. From the globular part of each joint arise a number of curved, radiating setæ.

The fly apparently does not feed at all, since no traces



FIG. 13 (  $\times 20$  ).

Side-view of male fly. The wing is extended and cut short; the legs cut short. The lower figure shows the genital armature in plan.

of food have been observed in its reduced alimentary canal, nor has it ever been seen to take in food. The mouth-parts (Fig. 12) are somewhat similar in arrangement to those of *Culex*, but are very largely atrophied. As in most Diptera, there is a roughly conical rostrum, which bears an elongated, triangular labrum, behind which is the short, bilobed labium. This is fringed with numerous,

\* Waterhouse (1895).

short, finger-like processes, and its edges are rolled forwards so as to enclose a pair of maxillæ. The maxillæ are short, styliform, and fringed with setæ; near the base they give rise to a pair of long, four-jointed maxillary palps. The styliform maxilla probably corresponds to the lacinia of typical forms; there does not appear to be anything to correspond to cardo and stipes. On the front of the labium is a minute, triangular hypopharynx or lingua.

*The Thorax of the Fly.*

As usual in Diptera, the thorax of *Psychoda* (Figs.

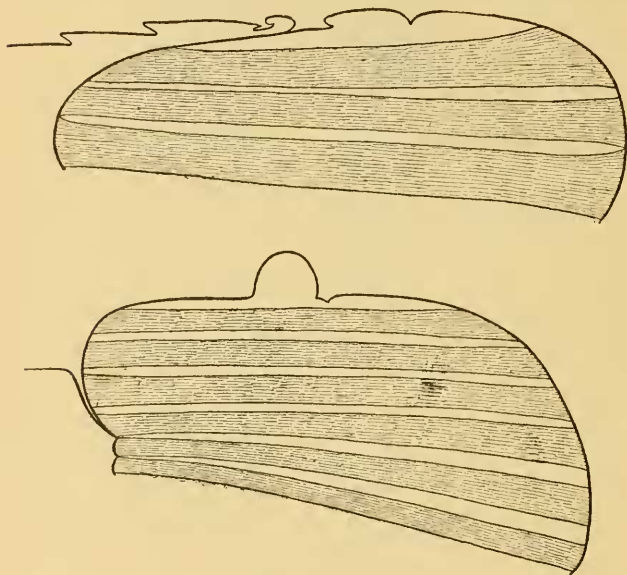


FIG. 14.

Longitudinal section of thorax of *Psychoda* (upper fig.); ditto of *Chironomus* (lower fig.).

13, 14) consists of a small prothorax, an enormous mesothorax, and a small metathorax. The prothorax is little more than a ventral hoop, containing the muscles of the first pair of legs. Ventrally and laterally its hinder margin is indicated by a suture. Dorsally its boundary is uncertain; it certainly, however, lies in front of the first spiracle.

The relations of the component parts of the mesothorax are peculiar, as will be seen by comparison with the corresponding structures in *Chironomus* (Fig. 14). In that type the dorsal region of the mesothorax consists of a large shield-shaped piece, the scutum; a transverse, semi-cylindrical ridge, arching across the back, the scutellum; and behind this a large postscutellum, to which the hinder ends of the longitudinal mesothoracic muscles are attached.\*

In *Psychoda* the same parts are found with the following points of difference:—

(1) The scutum extends forwards above the head, so that the head and prothorax are depressed to the ventral side, and the face looks downwards.

(2) In *Chironomus* the post-scutellum has extended backwards so far as to obliterate the dorsal part of the metathorax. In *Psychoda* the post-scutellum extends back quite as far as in *Chironomus*, but underlies the metathorax and the dorsal part of the first and second abdominal segments. It thus appears in longitudinal section as an enormous dorsal invagination of the cuticle, running backwards and downwards into the body as far as the hinder end of the second abdominal segment. I am informed by Mr. T. H. Taylor that a somewhat similar state of things is found in *Simulium*.

The dorsal part of the metathorax is a narrow strip, arching across the back immediately behind the scutellum. At the sides of the metathorax are the club-shaped halteres, or rudimentary second pair of wings, and the metathoracic spiracles.

The mesothorax is chiefly occupied by the muscles of flight, which are of extraordinary size, the longitudinal muscles, for instance, being half as long as the body.

There are two pairs of spiracles. The anterior, which is mesothoracic,† is formed at the place where the tracheal extension from the pupal respiratory appendage enters the imaginal body. Just at this point the cuticle of the fly thickens into a partial ring, while immediately distal to it

\* Miall and Hammond (1900).

† Voss (1905, p. 739) concludes from his study of *Gryllus domesticus* that the thoracic spiracles are probably prothoracic and mesothoracic. Miall and Hammond, on the other hand, find that they are mesothoracic and metathoracic in *Chironomus*, while Taylor (1902) comes to the same conclusion in his paper on *Simulium*.

the tracheal extension is thinner than anywhere else, and lacks the annular thickenings. This appears to be an arrangement for snapping the tracheal extension just at the required spot. Whether the pupal tracheæ persist as those of the adult, or whether all those of the thorax are withdrawn through the adult metathoracic spiracle, I am unable to say, but in all pupal skins hitherto examined no trace of tracheæ could be discovered, while the end of the tracheal extension always appeared to have been snapped across just where it originally entered the imaginal thorax. The metathoracic spiracle is a small, circular opening immediately below the base of the haltere.

*The Abdomen of the Fly and its Appendages (Fig. 13).*

The abdomen consists of eight segments. The first of these is only distinguishable dorsally, being ventrally obscured by the bases of the metathoracic legs. The seventh segment shows some indication of being divided into two parts. The last (eighth) segment in the male is flattened from above downwards, and slightly bifurcated at its hinder end, from which arises a long forceps, reaching forwards when at rest as far as the middle of the seventh segment. It is composed of two joints, a large basal and a small terminal one. From the fore end of the eighth segment arises a second forceps, also two-jointed. This runs upwards and backwards, and is enclosed by the other. There are also two processes arising from the hinder end of the seventh segment in the middle line; one is dorsal to the other. They are possibly analogous in function to the penis and titillator of a cockroach.

In conclusion, I desire to express my indebtedness to Professor Miall, at whose suggestion the work was first taken up, and without whose assistance and encouragement it could never have been carried out, and also to Mr. T. H. Taylor for much helpful advice and criticism.

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